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Hitching a ride: the formation locomotion strategy of dolphin calves

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Summary

1. Formation locomotion theoretically provides energy savings and it is evident across diverse taxa. Echelon position, described in cetacean (dolphin and whale) mother–infant dyads as calf in very close proximity of its mother's mid-lateral flank, may be a type of formation locomotion that provides hydrodynamic benefits for the calf. Until now, the difficulties associated with assessing the swimming energetics of marine mammals have precluded empirical quantifications of these benefits.
2. Through kinematic analyses, this study demonstrates empirically that 0–1 month-old dolphin (*Tursiops truncatus*) calves in echelon position are afforded locomotor advantages as evident by increased swim performance with concurrent reductions in effort.
3. Compared to periods of independent swimming, calves in echelon position showed a 28% increase in average swim speed with reduced effort during stroke phases, as evident by a 22% reduction in fluke stroke amplitude and 19% increase in distance per stroke.
4. In addition, calves in echelon position spent over a third of their time gliding while no glide phases were observed for independently swimming calves.
5. The hydrodynamic benefits of echelon position enable cetacean calves, which have extremely limited locomotor performance, to maintain proximity of their mothers during travel, which is vital to infant survival.
6. This study adds to the limited empirical data regarding the energy economy of formation locomotion in animals.

Key-words: cetaceans, echelon position, hydrodynamics, stroke and glide propulsion, swimming kinematics

Introduction

Formation locomotion is evident across diverse taxa in aquatic and aerial environments and can serve two functions, social (i.e. Hamilton 1967; Pitcher, Magurran & Winfield 1982) and/or energetic (i.e. Breder 1965; Lissaman & Schollenberger 1970) advantages. Although applied to all modes of locomotion including walking (Fancy & White 1985), saving energy by moving in formation is considered most practical in swimming (Breder 1965; Weihs 1973) and flying (Lissaman & Schollenberger 1970; Hummel 1983). Energetic advantages are possible because animals set the fluid around them moving (water or air) and these fluid movements in some circumstances can be taken advantage of by another individual to decrease their energy cost of locomotion (for review, see Alexander 2004). The energy savings of formation locomotion are predominately supported by theoretical work (i.e. Breder 1965, 1976; Belyayev & Zuyev 1969; Lissaman & Schollenberger 1970; Weihs 1973; Hidgon & Corrsin 1978; Badgerow & Hainsworth 1981; Hummel 1983, 1995; Kshatriya & Blake 1992) while empirical quantifications are rare. Only a few studies have measured oxygen consumption rate (Parker 1973; Abrahams & Colgan 1985; Fish 1994; Herskin & Steffensen 1998), heart rate (Weimerskirch *et al*. 2001), and wing (Hainsworth 1987; Weimerskirch *et al*. 2001), leg (Fish 1995) or tail (Zuyev & Belyayev 1970; Fields 1990; Fish, Fegely & Xanthopoulos 1991; Herskin & Steffensen 1998) beat frequency as a quantitative assessment of reduced effort during formation locomotion, and these measurements have been limited to fish and birds.

Echelon position (Fig. 1) is the predominant behaviour displayed by cetacean mother–infant dyads (McBride & Kritzler 1951; Tavolga & Essapian 1957; Norris & Prescott 1961; Au & Perryman 1982; Taber & Thomas 1982; Mann & Smuts 1999; Noren & Edwards 2007) and undoubtedly plays a social role in these dyads, but it may also provide an energetic

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Fig. 1. Bottlenose dolphin mother–calf pair swimming in echelon position. Echelon position is described as calf in very close proximity with its mother's mid-lateral flank in the region near her dorsal fin.

Fig. 2. A tracing from a digitized video clip of a 26-day-old calf swimming independently. Anatomical points of interest (rostrum tip, cranial insertion of the dorsal fin and fluke tip) were digitized at a rate of 60 fields per second of video using a motion-analysis system (Peak Motus 6·1; Peak Performance Technologies, Inc. Englewood, CO, USA) following methods similar to Skrovan *et al.* (1999) and Noren *et al.* (2006). A distinct trace represents the movements of each digitized anatomical point. From left to right, the trace from the rostrum leads (pink), followed by the trace from the cranial insertion of the dorsal fin (yellow), and last is the trace from the fluke tip (blue). The brown dot is a digitized reference point indicating that the camera was steady while filming this video clip.

advantage for the infant (Norris & Prescott 1961). Like many young eutherian mammals (Carrier 1996), cetacean calves are handicapped by small body size, undeveloped tissues, and naïveté and as a result have extremely limited locomotor performance (Noren, Biedenbach & Edwards 2006). Yet unlike some mammals whose offspring adopt a 'park' and hide strategy (Ross 2001), cetacean calves are required to maintain proximity of their mothers while she manoeuvres within their habitat to forage and avoid predators. Infant carrying behaviour is typical for animals that are required to accommodate their young offspring while travelling in aerial (i.e. bats) and arboreal (i.e. primates) environments (Ross 2001). Echelon position may provide a similar solution for animals travelling with young offspring in an aquatic environment. It has been hypothesized that echelon position enables calves to travel at adult speed (Norris & Prescott 1961) by theoretically minimizing the calf's cost of transport as it is carried in its mother's pressure wave (Kelly 1959; Weihs 2004). Although echelon position could increase the swim performance of dolphin calves (present study), it may at the same time increase maternal swimming costs (Noren 2008). The difficulties of assessing the swimming energetics of marine mammals, particularly cetacean mother–calf pairs, had previously precluded empirical quantifications of the benefits of this behaviour for the calf and the costs of this behaviour for the mother.

Current interactions between dolphins and tuna-purse seine fisheries in the eastern tropical Pacific Ocean (ETP) makes the study of dolphin mother–calf swimming especially timely. These fisheries capture schools of yellowfin tuna (*Thunnus albacares*) by locating, chasing and encircling herds of associated dolphins. Fishery interactions are prolonged, during which dolphins elevate routine speeds of 1 m s^{-1} to chase and burst speeds of 2–4 and 5–8 m s^{-1}, respectively (Au & Perryman 1982; Au, Scott & Perryman 1988; Chivers & Scott 2002). Despite reduced observed dolphin mortality associated with this fishery, dolphin populations are not recovering (Gerrodette & Forcada 2005). A contributing factor may be the disruption of echelon position during chase and the subsequent permanent separation of the mother–infant dyad (Noren & Edwards 2007). To elucidate the benefits gained by calves maintaining echelon position, we examined the kinematics of dolphin calves swimming in echelon (Fig. 1) and swimming independent of their mothers (> 1 m from other dolphins) to provide the first empirical quantification of this formation locomotion strategy. An examination of the swimming kinematics of dolphin mothers swimming in echelon and swimming solitarily is provided in the accompanying article (Noren 2008).

Materials and methods

Three captive bottlenose dolphin (*Tursiops truncatus*) mother–calf pairs provided a controlled experimental approach to investigate cetacean locomotor effort and performance (Fish 1993; Skrovan *et al.* 1999; Noren *et al.* 2006). A stationary submerged SCUBA diver with a digital video camcorder (Sony Hi-8, Sony, Oradell, NJ, USA) in an underwater housing (Amphibico Dive Buddy, Amphibico, Montreal, Quebec, Canada) videotaped dolphins swimming in a large natural lagoon (43 × 53 × 7 m deep) at Dolphin Quest Hawaii during daylight hour. The animals swam 0·5–1·0 m below the surface of the water and swam within 7–8 m in front of the SCUBA diver. Experimental swim sessions included both opportunistic (no reward) and directional swimming between two trainers (reward based). Videotape of calf swimming was acquired over 3 weeks when the calves were 0–34 days postpartum. Fifteen hours of swimming were recorded and 425 short 1–6 s video clips were extracted and digitized (Fig. 2). Clips were divided into two association categories: (i) echelon position (Fig. 1); and (ii) independent swimming (calf > 1 m away from all dolphins). Clips were further categorized as either calf gliding or stroking.

A quantitative assessment of swim effort was obtained by calculating peak-to-peak fluke stroke amplitude and tailbeat oscillation frequency.

Higher amplitudes and frequencies are associated with greater energy expenditure (Kooyman & Ponganis 1998). Normalized tailbeat frequency (ratio of tailbeat frequency to swim speed; Rohr & Fish 2004) and distance per stroke were also calculated. Methods for video analysis and swim effort calculations are described in detail elsewhere (Noren *et al.* 2006).

The goal of this study was not to address individual variation, but to quantify changes in locomotor performance associated with swim style (echelon vs. independent), thus similar to other kinematic studies data across individuals were pooled (Fish 1993; Skrovan *et al.* 1999; Noren *et al.* 2006). Pearson product moment correlations were used to determine the correlation of the swimming kinematics (fluke stroke amplitude and tailbeat frequency) with swim speed for echelon swimming and also for independent swimming; linear regression analyses were then used to determine the relationship for the parameters that demonstrated a strong correlation. In cases where the swimming kinematics were significantly correlated with swim speed, an analysis of covariance (Generalized Linear Model, GLM) was used to determine which variable(s) (swim speed, swim position, and the interaction of swim speed and swim position) affected the swimming kinematics. Swim speed, fluke stroke amplitude, normalized tailbeat frequency, and distance per stroke during echelon swimming and independent swimming were compared using Mann–Whitney Rank Sum Tests because normality failed. Size-specific fluke stroke amplitude was compared using student's *t*-test. Statistical analyses were performed using Sigma Stat 2·03 and Systat 10·2 (Systat Software, Inc. Point Richmond, CA, USA). Means ± 1 SEM are presented and $\alpha = 0{\cdot}05$.

Results

Our experimental approach adequately captured swimming behaviours representative of wild dolphins. This was evident by the similarity in experimental swim speeds (0·58–4·47 m s^{-1}; present study) to the optimal range (1·7–2·3 m s^{-1}, Williams *et al.* 1993; 1·9–3·2 m s^{-1}, Yazdi, Kilan & Culik 1999) and observed sustainable (3·1 m s^{-1}; Lang 1975) swim speeds of adult bottlenose dolphins. In addition, the proportion of time spent in echelon position was similar for experimental calves (60% of time; assuming that the clips represented a random sample) and 0–1 month-old wild calves (69·3% of time; Mann & Smuts 1999).

Calves in echelon position maintained elevated swim speeds compared to periods of independent swimming (Fig. 3a). The swim speeds of calves in echelon (range: 0·69–4·47 m s^{-1}, median: 1·65 m s^{-1}, mean swim speed: 1·83 ± 0·04 m s^{-1} or 1·51 ± 0·04 body lengths per second, $n = 256$) significantly exceeded ($T = 27962{\cdot}500$, $P < 0{\cdot}001$) those of calves swimming independently (range: 0·58–4·20 m s^{-1}, median: 1·34 m s^{-1}, mean swim speed: 1·43 ± 0·04 m s^{-1} or 1·19 ± 0·03 body lengths per second, $n = 169$). The difference in swim speed was not associated with the motivation of the calves, because in all instances calves were actively trying to maintain proximity of their mothers. Interestingly, the ages that comprised the echelon category (range: 0–34 days, median = 9 days, mean = 12 ± 0·6 days, $n = 256$) were significantly lower ($T = 43317{\cdot}500$, $P < 0{\cdot}001$) than those comprising the independent swimming category (range: 0–34 days, median = 18 days, mean = 18 ± 0·8 days, $n = 169$).

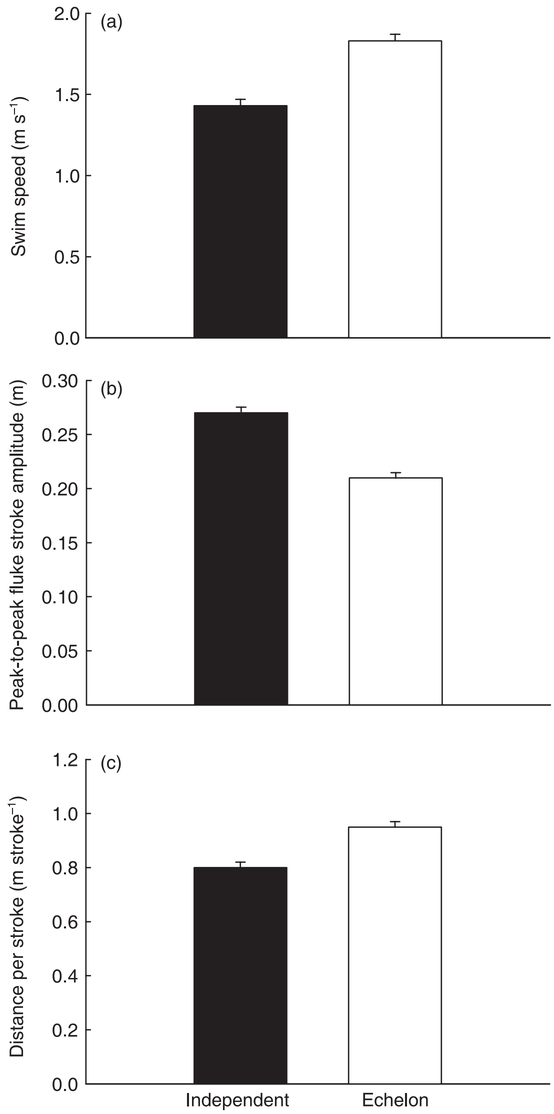

Fig. 3. Swim performance of dolphin calves was improved by the hydrodynamic advantages gained through echelon position. The swim speed (a), fluke stroke amplitude (b), and distance covered per stroke (c) for calves stroking independently (black bars) and stroking in echelon (white bars) are presented. Compared to calves swimming independently, calves stroking in echelon were afforded significantly greater swim speeds with concurrent significant reductions in effort through reduced fluke stroke amplitudes and increased distance per stroke. See text for statistics.

Calves in echelon were also afforded energetic savings. Thirty-six percent of the clips depicting echelon position showed calves gliding. Assuming that the clips represented a random sample this result suggests that calves in echelon position spend over a third of their time moving forward through the water without moving their flukes. In contrast, there were no gliding periods observed for calves swimming independently.

Calves in echelon also gained energetic benefits during the stroke phase. Peak-to-peak fluke stroke amplitude was significantly lower ($T = 19893{\cdot}000$, $P < 0{\cdot}001$) for calves stroking in echelon (median fluke stroke amplitude = 0·21 m,

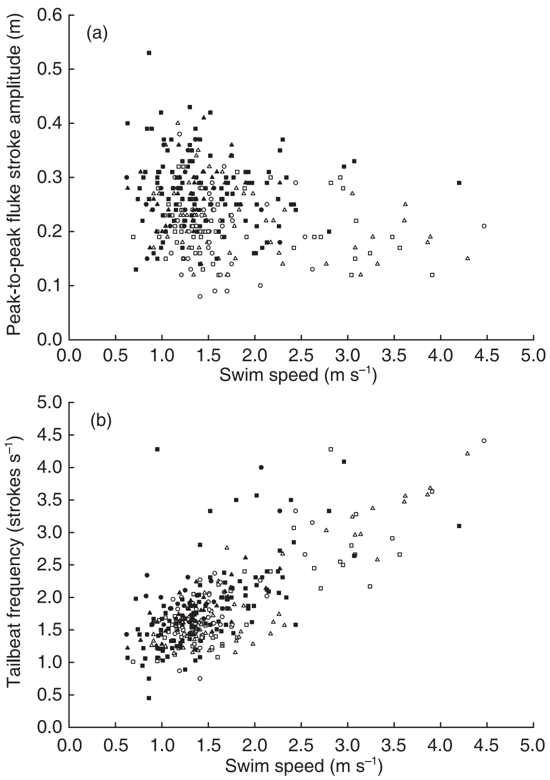

Fig. 4. Swimming kinematics of the calf in relation to the swimming speed of the calf. Peak-to-peak fluke stroke amplitude (a) was not correlated with swim speed for calves stroking independently (black symbols; $r = -0{\cdot}0382$, $P = 0{\cdot}628$, $n = 164$) or in echelon position (white symbols; $r = -0{\cdot}191$, $P = 0{\cdot}0145$, $n = 163$; weak negative correlation likely an artefact of limited samples for upper swim speeds). In contrast, tailbeat frequency (b) was significantly correlated with swim speed for calves stroking independently (black symbols; $r = 0{\cdot}624$, $P \leq 0{\cdot}001$, $n = 164$) and in echelon position (white symbols; $r = 0{\cdot}851$, $P \leq 0{\cdot}001$, $n = 163$). Given the strong linear correlation between swim speed and tailbeat frequency (SF), linear regressions are provided for echelon (speed = 0·92 SF + 0·05; $r^2 = 0{\cdot}724$, $F = 422{\cdot}583$, $P < 0{\cdot}001$) and independent (speed = 0·53 SF + 0·47; $r^2 = 0{\cdot}389$, $F = 103{\cdot}121$, $P < 0{\cdot}001$) swimming. A different symbol is used for each of the three individual dolphins.

mean fluke stroke amplitude: 0·21 ± 0·005 m, $n = 163$) compared to calves stroking independently (median fluke stroke amplitude = 0·27, mean fluke stroke amplitude = 0·27 ± 0·005 m, $n = 164$; Fig. 3b); peak-to-peak fluke stroke amplitude was compared directly across association categories because peak-to-peak fluke stroke amplitude was not correlated with swim speed for calves stroking either in echelon position or independently (Fig. 4a). Likewise, size-specific peak-to-peak fluke stroke amplitude was significantly lower ($t = 9{\cdot}010$, df = 325, $P < 0{\cdot}001$) for calves stroking in echelon (median fluke stroke amplitude = 17% body length, mean fluke stroke amplitude: 18 ± 0·004% body length, $n = 163$) compared to calves stroking independently (median fluke stroke amplitude = 22% body length, mean fluke stroke amplitude: 23 ± 0·004% body length, $n = 164$). In contrast to that found for peak-to-peak fluke stroke amplitude, tailbeat frequency was positively correlated with swim speed for calves stroking in echelon position and independently (Fig. 4b). The results of the GLM indicated that the interaction of swim speed and swim position did not have a significant affect on tailbeat frequency, but independently both swim speed ($F = 445{\cdot}524$) and swim position ($F = 21{\cdot}493$) each had a significant affect on tailbeat frequency ($n = 327$, $P < 0{\cdot}001$). Thus, normalized tailbeat frequency was compared. Normalized tailbeat frequency was significantly lower for calves stroking in echelon ($n = 163$) than for calves stroking independently ($n = 164$; $T = 21644{\cdot}000$, $P < 0{\cdot}001$) with the result that distance per stroke was significantly greater ($T = 31800{\cdot}000$, $P < 0{\cdot}001$) for calves stroking in echelon (median distance per stroke = 0·92 m stroke^{-1}, mean distance per stroke = 0·95 ± 0·02 m stroke^{-1}) compared to calves stroking independently (median distance per stroke = 0·79 m stroke^{-1}, mean distance per stroke = 0·80 ± 0·02 m stroke^{-1}; Fig. 3c).

Discussion

Formation locomotion may be an important strategy that ensures that cetacean mother–infant dyads remain intact during travel, which is vital to the survival of the offspring (for review, see Noren & Edwards 2007). Without the energetic advantages of formation locomotion it is unlikely that young calves can independently maintain swim performance levels similar to those of adults given the diminutive body size and underdeveloped musculature of cetacean calves (Noren *et al.* 2006; Noren & Edwards 2007). Maximum independent swim speeds of a newborn and 1-month-old calf in this study were only 0·57 and 1·00 times the observed sustainable swim speed of adult bottlenose dolphins (3·1 m s^{-1}; Lang 1975), respectively. The results of this study demonstrate that echelon swimming is a type of formation locomotion that provides hydrodynamic benefits to dolphin calves as this swimming strategy enabled the youngest, most underdeveloped calves to achieve improved performance (Fig. 3a). For example, a 2-day-old calf nearly doubled its maximum independent swim speed of 2·27 to 4·47 m s^{-1} while in echelon. Similarly, a 31-day-old calf increased maximum swim speed from 3·07 to 3·56 m s^{-1} with a change in association from independent to echelon. Overall, calves in echelon position maintained elevated swim speeds compared to periods of independent swimming (Fig. 3a).

These results have implications for dolphins that interact with tuna purse-seine fisheries in the ETP. Fishery related dolphin chase/release may last for several hours with speeds approaching 1·3–1·9 times normal adult ETP dolphin cruising speeds (calculated from Chivers & Scott 2002) while at the same time chase/release activity could disrupt echelon position (Weihs 2004). Given that 0–1 month-old calves cannot independently sustain adult cruising speeds (Noren *et al.* 2006), and that physiological development of ETP and bottlenose dolphin calves are similar (Noren & Edwards 2007), 0–1 month-old ETP calves could fall behind if echelon position is disrupted. This may explain the observation that 75%–95% of lactating females killed in tuna purse-seine nets were not accompanied by their calves (Archer *et al.* 2004).

Given the extreme intensity of this fishery, this cascade of events may partially explain the non-recovery of these depleted dolphin populations observed by Gerrodette & Forcada (2005).

In addition to attaining enhanced swim speeds, calves in echelon position were also afforded energetic savings. Prolonged periods of glide were evident for calves in echelon while no glide periods were observed for independently swimming calves. Although our methods precluded recording entire glide periods, the longest echelon glide clip recorded (4·65 s) greatly exceeded the 2-s glide periods recorded for unassisted horizontally steady state swimming adult dolphins (Skrovan *et al*. 1999). Likewise, fish demonstrated increased coast time when swimming in schools compared to periods of solitary swimming (Fish *et al*. 1991). Calves in echelon also gained energetic benefits during the stroke phase as evident by reduced fluke stroke amplitude and increased distance per stroke compared to periods of independent swimming (Fig. 3b,c). Similarly, birds in flight formation (Weimerskirch *et al*. 2001) and fish in schools (Fields 1990; Herskin & Steffensen 1998) demonstrated reduced effort during stroke phases as evident by reduced wing or tail beat frequency compared to periods of independent locomotion. Interestingly the size-specific fluke stroke amplitude of adult dolphins (20% body length; Fish 1993; Skrovan *et al*. 1999) was intermediate to those of calves stroking in echelon and calves stroking independently; calves stroking in echelon displaced their tailflukes relatively less than adults while independently stroking calves displaced their tailflukes relatively more than adults. Compared to adult swimming it appears that echelon swimming by calves is more economical while independent swimming by calves is more arduous. Neonatal dolphins manoeuvring independently may need to exert more effort than adults to overcome their compromised swimming efficiency associated with their extreme skeletal and muscular flexibility (Etnier *et al*. 2003), and floppy fins and flukes (McBride & Kritzler 1951; Tavolga & Essapian 1957).

Nonetheless it appears that immature dolphins have evolved a unique behavioural strategy to assist their swim performance. Echelon position enables calves to achieve elevated swim speeds with reduced effort compared to periods of independent swimming (Fig. 3). Likewise adult marine mammals utilize behavioural strategies to increase swim performance such as wave riding, porpoising and stroke-and-glide diving (reviewed by Williams 2001). The benefits gained by calves in echelon are similar to those gained by adult marine mammals (Williams *et al*. 1992, 2000), aquatic birds (Stephenson 1994; Lovvorn, Croll & Liggins 1999), and fish (Weihs 1974) that utilize stroke and glide propulsion to decrease effort and improve performance. For adult marine mammals and fish, the low drag associated with gliding periods during intermittent swimming compensates for the increased effort of re-acceleration during stroke phases (Weihs 1974; Videler 1981; Blake 1983). However, unlike individual travellers, which only gain advantages during glide phases, dolphin calves in echelon gain additional energetic savings during stroke phases. Calves in echelon realized an average 22% reduction in fluke stroke amplitude and 19% increase in distance covered per stroke compared to periods of independent swimming (Fig. 3b,c). Likewise, paddling ducklings reduced arc length (Fish 1995) and swimming fish decreased tailbeat frequency (Herskin & Steffensen 1998) when manoeuvring in formation compared to solitary swimming. Dolphin calves, like ducklings and fish, are able to extract energy from environmental vortices that arise from fluid flow from the propulsive movements of other animals (Kelly 1959; Weihs 2004). Theoretically the youngest dolphin calves gain the most benefits from echelon position because of the size disparity between the mother and neonate (Weihs 2004).

In summary, we provide the first empirical quantification that supports the 50-year-old hypothesis that echelon position enables calves to maintain adult speeds with reduced locomotor effort (Norris & Prescott 1961). Given the limited swimming capabilities of independently swimming 0–1 month-old dolphin calves, it is unlikely that calves are able to stay in proximity of their mothers during travel in the absence of echelon position. Consequently this formation swim strategy is vital to infant survival. The results of this study provide insight into how tuna purse-seine fishery interactions may impact survival rates of dolphin calves in the ETP and add to the limited empirical quantifications of the energy economy of formation locomotion in animals.

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